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Evolution: Postponing Extinction by Polyandry

Sex-ratio meiotic drive occurs when males produce a predominance of X-chromosome bearing sperm and an inordinate number of daughters. A driving X causes highly female-biased sex ratios and the risk of extinction. Polyandry can rescue a population from extinction.

Michael J. Wade

Meiotic drive is the failure of 'fair' Mendelian meiosis in heterozygous individuals, such that they produce gametes carrying a preponderance of one allele instead of the expected equal proportions of two alleles. Meiotic drive can be detected only in the progeny of heterozygotes and only if one allele produces a recognizable phenotype. Meiotic drive involving a sex chromosome, X^{SR} (where the superscript 'SR' stands for sex ratio), is easy to detect, because every mating involves a heterozygote (males are the heterogametic or XY sex in many species, including fruit flies), the sex of an offspring is a readily recognizable phenotype, and the expected ratio of sons to daughters is 1:1. Mendelian meiosis results in males producing equal numbers of X-chromosome bearing and Y-chromosome bearing sperm, while XX females produce only X-bearing eggs. Meiotic drive is a violation of Mendelian meiosis such that $X^{SR}Y$ males produce almost exclusively X^{SR} sperm and few if any Y-bearing sperm. As a result, their offspring are overwhelmingly daughters and few, if any, sons. In a population, the selective advantage of a driving X^{SR} relative to a wild-type X-chromosome is nearly two-fold, making sex-ratio meiotic drive one of the strongest known evolutionary forces. In theory, the population sex ratio is a simple function of the frequency of X^{SR}. As the X^{SR} chromosome spreads relentlessly, it would ultimately result in a population composed entirely of females, which will go extinct [1–3]. However, the observed frequency of X^{SR} in natural populations is low: less than 25% in natural populations of *Drosophila peudoobscura* [4]. Furthermore, in laboratory experiments, the frequency of X^{SR} often tends to decline [5] and extinction takes place rarely or never. This gives rise to the question that has absorbed research geneticists for decades: what are the evolutionary forces that limit meiotic drive? The study of meiotic drive offers the rare opportunity to investigate conflict between opposing selective forces and between different levels of selection (gametic, individual and group) while the evolutionary conflict is in progress.

An experimental study by Trevor Price, Gregory Hurst and Nina Wedell [6], published in this issue of *Current Biology*, marks an important step forward in our understanding of the evolutionary forces that limit the effects of meiotic drive. Their work rests on the earlier observations [7] that discovered that in *Drosophila peudoobscura* males with an X^{SR}-chromosome ($X^{SR}Y$ males) produce only half the amount of functional sperm of normal, $X^{+}Y$ males (where X^{+} indicates a normal, wild-type X-chromosome). Mechanistically, it turns out that, in the development of the gametes of $X^{SR}Y$ males, X^{SR} bearing sperm survive at the expense of Y-bearing sperm, reducing by half the total amount of functional sperm. Thus, the mechanism responsible for the apparent meiotic drive appears to contain the seeds for its own limitation in that $X^{SR}Y$ males will suffer a severe handicap in reproductive competition with normal males because they have fewer sperm. However, early research into the sperm competitive ability or 'virility' of $X^{SR}Y$ relative to $X^{+}Y$ males was conflicting or ambiguous [8–12] and models showed that the expected fitness effects, especially in the presence of frequency-dependent mating and re-mating, should be complex [12–15] with the possibility of multiple, stable intermediate equilibria.

In their study, Price and colleagues [6] established 48 populations using *D. peudoobscura* recently isolated from a wild population, each with a frequency of 30% of the X^{SR} chromosome, mirroring the natural frequency in their source population. Each population was founded with 60 males and 60 females and subsets of 12 populations were subjected to different and artificially controlled mating treatments. In the monandrous treatment, sexually mature females were mixed with males for four hours before being isolated away from males — it is known that females will

mate only once under these conditions. In the other treatments polyandry was encouraged and females were given two, three, or six additional mating bouts. Over the course of the 15 generations the experiment lasted, the number of monandrous populations decreased from 12 to 7, and the cause of these extinctions was the lack of production of functional males. Furthermore, the frequency of X^{SR} in the surviving monandrous populations was significantly higher than that in each of the polyandry treatments (in which the frequencies were not different from one another). The authors conclude that, although all of the offspring of $X^{SR}Y$ males inherit the X^{SR} chromosome, these males produce far fewer offspring than a normal male when females mate multiple times and polyandry allows for sperm competition between males within the reproductive tracts of females. Their results also suggest that local extinction of populations with very high frequencies of the X^{SR} chromosome might be an additional evolutionary force restricting the female-biased sex ratios generated by the meiotic drive.

These findings are novel and important because they illustrate that sexual selection via reproductive competition between males is a strong evolutionary force acting in the opposite direction to and limiting the effects of meiotic drive; together, these opposing forces can establish the polymorphisms seen in nature. Nevertheless, there remains a great deal of additional research to be conducted on this and other meiotic drive systems. It has, for instance, been shown that $X^{SR}X^{SR}$ homozygous females may suffer reduced viability and, in theory, such sexually antagonistic effects of viability selection acting against the spread of the X^{SR} chromosome are sufficient to sustain polymorphism. Such effects may have been present in the experimental cultures of Trevor Price and colleagues, and are even suggested by the periodicity in the frequency of males in the later generations of the polyandrous treatments [6]. In addition, natural populations of this species of fly tend to be considerably more abundant as well as open to migration relative to the closed laboratory populations. Nevertheless, the new study [6] reports a striking set of replicated observations using flies recently derived from nature that not only exhibits frequent, sex-ratio biased caused extinctions, but also a clear rescuing effect of polyandry.

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Transcriptional Memory: Mothers SET the Table for Daughters

Eukaryotic gene transcription within individual cells of a population is often associated with heterogeneous pulses of gene activity. A recent study, however, shows that mothers and their daughters share similar transcriptional frequencies, and inheritance of mother's transcriptional tendencies requires methylation of histone H3 by a Set1 methyltransferase.

Craig L. Peterson

Establishing and maintaining transcriptional states that are heritable to progeny plays a central role during development of multi-cellular organisms. In some cases a transcriptional state is propagated in the absence of the original inducing signal, suggesting some type of transcriptional 'memory'. Perhaps the most widely accepted example of transcriptional memory occurs at homeotic genes where spatial expression patterns are maintained throughout the life of the organism in the absence of the initial segmentation gene products that established the initial transcription states [1]. Likewise, unicellular eukaryotes rapidly adapt to signals from their microenvironment by altering their transcriptional profile, and the ability to pass on a memory of such altered environmental conditions may provide progeny with a selective advantage. Since these heritable changes in gene expression do not involve alterations to an organism's genome, they represent examples of epigenetic regulation.

Over the past ten years, use of the word 'epigenetic' has become synonymous with studies of chromatin structure and function. In particular, patterns of histone post-translational modifications have been suggested to provide a type of code for ON/OFF states of gene expression that might self-propagate during cell division and thus provide heritable marks for gene expression states. Although this view has remained pervasive, histone modifications are generally dynamic, are not self-propagating,